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Evolution of the Morphology of Bottom Walking Turtles

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by

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Abstract

Ecomorphology and functional morphology are two distinct disciplines within biology that are often conflated and erroneously used interchangeably. By investigating the morphological distinctiveness of bottom-walking turtles relative to aquatic swimmers and terrestrial walkers, we can disentangle the effects of ecology and performance. Shell morphology, tail length, digit length, webbing length, and integumental differences were examined using dry and wet preserved specimens. Bottom-walkers were hypothesized to be distinct in all measurements. Instead, bottom-walkers were typically distinct from terrestrial taxa but not aquatic taxa, although for integumentary structures, only bottom-walkers were found to have significantly more integumentary structures than terrestrial turtles. This demonstrates that, despite sometimes highly differential locomotor modes, ecology, defined as habitat type, can show a stronger morphological signal than function.

Introduction

Ecological morphology and functional morphology are both well-established fields of inquiry in biology. Ecomorphology studies the environmental influences upon an animal's morphology (Wainwright and Reilly, 1994), and functional morphology defines the behavior and use of structure and how it affects morphology. Ecomorphology searches for correlations between habitat and morphology, and functional morphology searches for correlations between function and morphology. These fields often overlap and even more often are conflated - ecomorphological patterns are often explained by reference to function, and functional differences are often approximated by differences in ecology. While such overlap is most likely very common, the two are not interchangeable. Organisms can live in different environments, while selection acts to optimize similar functions, and organisms can utilize different functions in the same environment. For example, organisms can use many different forms of locomotion within the same medium. Aquatic organisms can swim or walk along the bottom of waterways; organisms living in water or on land can both locomote via walking.

Despite the large numbers of both ecomorphological and functional morphological studies (Schöning et al., 2005; Camp et al. 2007), attempts are only infrequently made to relate the two. More often, functional interpretations are given to ecomorphological patterns, and not tested. For example, the sandfish, *Scincus scincus*, is a terrestrial lizard that has been assumed to walk as typical terrestrial lizards do, however, the sandfish actually swims through sand (Baumgartner, 2008). Functional differences are also assumed to reflect ecology.

For example, elephants are the largest living land animals and, despite being unable to run or jump, these animals are proficient swimmers (Johnson, 1980). Thus, many times it is unclear whether habitat or function will show the greater predictive power with regards to morphology. For example, in the example above – organisms living in similar environments but locomoting differently - does an organism's environment or its mode of locomotion have more influence in determining its morphology? It is well known that both ecology and locomotor mode can influence morphology in certain species. Animals may change to allow more efficient or faster locomotion, based on any number of initial selective pressures. Previous work (Munteanu and Stayton, 2011) showed that terrestrial turtles, which locomote solely via walking, have narrower plastrons (bottom parts of the shells) than aquatic turtles, which were assumed to locomote via swimming. These patterns were seemingly in accordance with locomotor mode - terrestrial turtles must angle their limbs to counteract gravity, while aquatic turtles do not have this same selective pressure. Additionally, aquatic turtles showed shorter bridges (which would aid in greater laterally-directed swimming stroke), which is in accordance with using a swimming locomotor mode. Within the same study, and in numerous previous studies (Claude, 2003; Rivera, 2008) ecomorphological patterns in shell shape have been documented - the shells of aquatic turtles, whether or not those species locomote by swimming or bottom-walking, have been found to be flatter and more streamlined than terrestrial turtles, possibly due to conflicting selective pressures for the functions of shell strength and hydrodynamic efficiency. Differences are even found in narrower ecological categories: morphological differences have been

found in shell shape between populations of one turtle species that were found in either slow moving (lentic) or fast moving (lotic) waterways. (Rivera, 2008) This study further demonstrates how hydrodynamicity is a strong ecological selective pressure, but is also an example of how ecomorphological patterns are often assumed to reflect functional performance.

As these examples illustrate, locomotion makes an excellent system within which to dissect the semi-independent effects of ecological habitat and function, and turtles make for excellent model organisms in comparative morphological studies. Turtles have a rigid, bony shell that is well suited for quantitative analyses. These attributes make this group of animals an excellent subject for the study of morphological diversification in response to ecological and environmental selective pressures. Indeed, turtles have been used in numerous previous ecomorphological and functional studies (Rivera, 2008; Stayton, 2009; Stayton, 2011).

A subgroup of aquatic turtles, the bottom walkers, provides a unique opportunity to dissect the influences of locomotor function and ecology on morphological evolution. Bottom-walkers are, as the name suggests, aquatic turtles that walk on the bottom of rivers, lakes, and other types of waterways. These animals are often not found to be swimming. Bottom-walkers have not been the subject of many previous ecological or functional morphological studies. Bottom-walking turtles may or may not be subject to the same selective pressures as other aquatic turtles; bottom-walking turtles spend much less time swimming through water (Willey and Blob, 2004) and usually inhabit slow-moving waterways, possibly reducing the pressure to maintain a hydrodynamic shell similar to other aquatic

turtles. Investigating this group of turtles may help disentangle ecology and function because this group shares ecology with swimming turtles, as well as sharing function with terrestrial turtles. In addition, this work will provide much-needed data to characterize an understudied locomotor mode within vertebrates.

In fact, most data on bottom-walking turtles are merely anecdotal. Such species are assumed to swim very infrequently (Willey and Blob, 2004) Bottom-walkers are believed to often have similarly narrow plastrons, particularly within mud turtles (Kinosternidae) and snappers (Chelydridae). It has been hypothesized that these reduced, cruciform plastron evolved to ease the energetic expenditure for across-land migration (Zhu, 2011). Considering that bottom-walking turtles locomote in a style reminiscent of terrestrial locomotion, it would be interesting to see if plastra (and shell as a whole) showed the same trend across all turtles that regularly employ walking, regardless of environment.

The goal of this study is to address the question: what are the relative magnitudes of the effects of ecological habitat and locomotor mode on morphology? Specifically, this study will analyze bottom-walking turtles to determine if members of the group are more similar to species with which they share a common ecology (aquatic swimmers), or to those with which they share a common locomotor mode (terrestrial walkers), in terms of a number of morphological characteristicsincluding shell morphology, tail length, and various integumental structures.

The following hypotheses were tested: H1 – bottom-walking turtles are distinct, morphologically, from other aquatic turtles, but their shells are more

similar to the shells of terrestrial species than to the shells of swimming species. Bottom-walkers use a terrestrial locomotive strategy in an aquatic environment. Locomotive strategy and habitat both influence shell morphology (Rivera, 2008). Walking locomotion and aquatic habitat is a unique combination of selective pressures, and should in turn make bottom walkers distinguishable from other aquatic turtles as well as terrestrial turtles. Additionally, bottom-walkers inhabit slow-moving waterways (as do many swimming aquatic turtles), and selection for hydrodynamics may be relaxed on this subgroup to optimize strength; between aquatic and terrestrial turtle shells, bottom-walker shells should more closely resemble terrestrial turtle shells because the locomotor selective pressure will have greater influence.

H2 – bottom-walking turtle tail length will be significantly longer than that of other groups. The basis for this hypothesis is anecdotal: many turtles, especially within snappers, have relatively larger and longer tails than other species. Preliminary results (H. Ruiz, *pers. comm.*) on tail length in bottom-walkers suggest significant differences, albeit among a small sample of species.

H3 – bottom-walking turtles will have significantly *more* integumental features on their bodies than other groups. Both improved sensation and crypsis are advantages associated with integumental processes. Integumental process evolution would aid in tactile sensitivity in riverbeds and other waterway bottoms, where visibility is particularly low. Integumental processes also aid in breaking up the outline of the animal, facilitating crypsis. However, these structures also might produce a trade-off with hydrodynamicity. Streamlined bodies in a fluid do not have

such protrusions, because it can encourage eddy production, which can cause drag. In species in which these are present, swimming is not a primary mode of locomotion or that fast swimming is not a priority.

H4 – bottom-walkers will have significantly *less* pes digital webbing than other groups, especially the aquatic, swimming species. Drag-based swimming, prevalent in non-marine aquatic turtles, involves the use of the alternating limb propulsion for locomotion (Stein, 2005). If bottom-walkers do not use swimming as a primary mode of locomotion, the webbing of the pes should be less extensive than that of aquatic, swimming species, but more than that of terrestrial species.

H5- bottom-walkers will have significantly shorter pes digits. This follows the same progression as H4; if swimming propulsion is not a locomotor priority (as predicted), the digits for the pes will be less paddle-like.

Materials and Methods

All turtle species (n=324) were categorized into one of four groups: bottom-walking (bw), aquatic (aq), terrestrial (te), or marine (ma), based off of the habitat descriptions in Bonin, Devaux, and Dupre (2006).

Data Collection

Morphological data consisted of digitized X-, Y-, and Z- coordinates corresponding to 59 landmarks on the shells of 280 turtle specimens in 237 species

(Fig. 1).

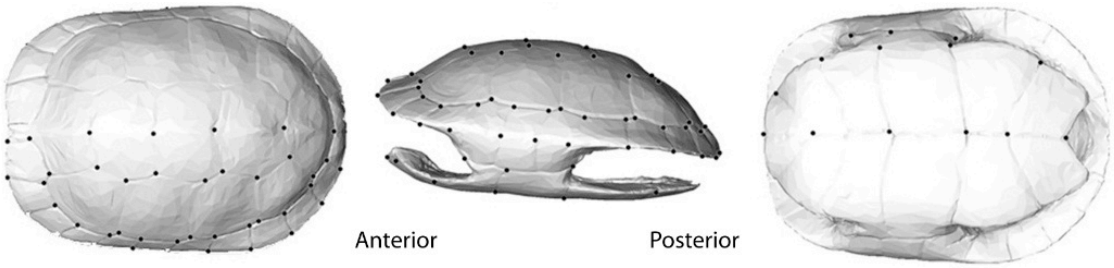

Fig. 1 – A model shell of *Glyptemys muhlenbergii* marked with landmarks (modified from Stayton 2009).

Specimens were obtained from a number of museums, including the American Museum of Natural History (New York, NY), Carnegie Museum of Natural History (Pittsburgh, PA), Cornell University Museum of Vertebrates (Ithaca, NY), Field Museum of Natural History (Chicago, IL), Museum of Comparative Zoology (Cambridge, MA), and the National Museum of Natural History (Smithsonian, Washington, DC). Specimens were photographed in dorsal, lateral, and ventral views using a Nikon Coolpix 5400 digital camera (Nikon Corp., Tokyo, Japan). Whenever possible, multiple specimens, including both males and females, of all species were used. Digitization of pictures was performed in the program tpsDig (Rohlf FJ, 2006). Two-dimensional images of each axis were combined into a three-dimensional image using a custom program written for MATLAB (Stayton, 2009). Some specimens were also digitized using a Microscribe G2X digitization system.

Tail length data was collected from museum specimens at the Smithsonian Museum Support Center in Suitland, Maryland. Tail length (TL) and curved carapace length (CCL) were measured on all specimens. TL was measured from the tip of the tail, to the point at which the tail skin joined the plastron. CCL was

measured from the most anterior part of the nuchal scute, down the dorsosagittal plane, and ending at the most posterior portion of the caudal scute.

Webbing on the second and third digit of the pes was also measured on wet specimens. The distance from the metatarsophalangeal joint until the end of the interdigital webbing between the second and third digit was measured. Full digit length was also measured for comparison. (Fig. 2)

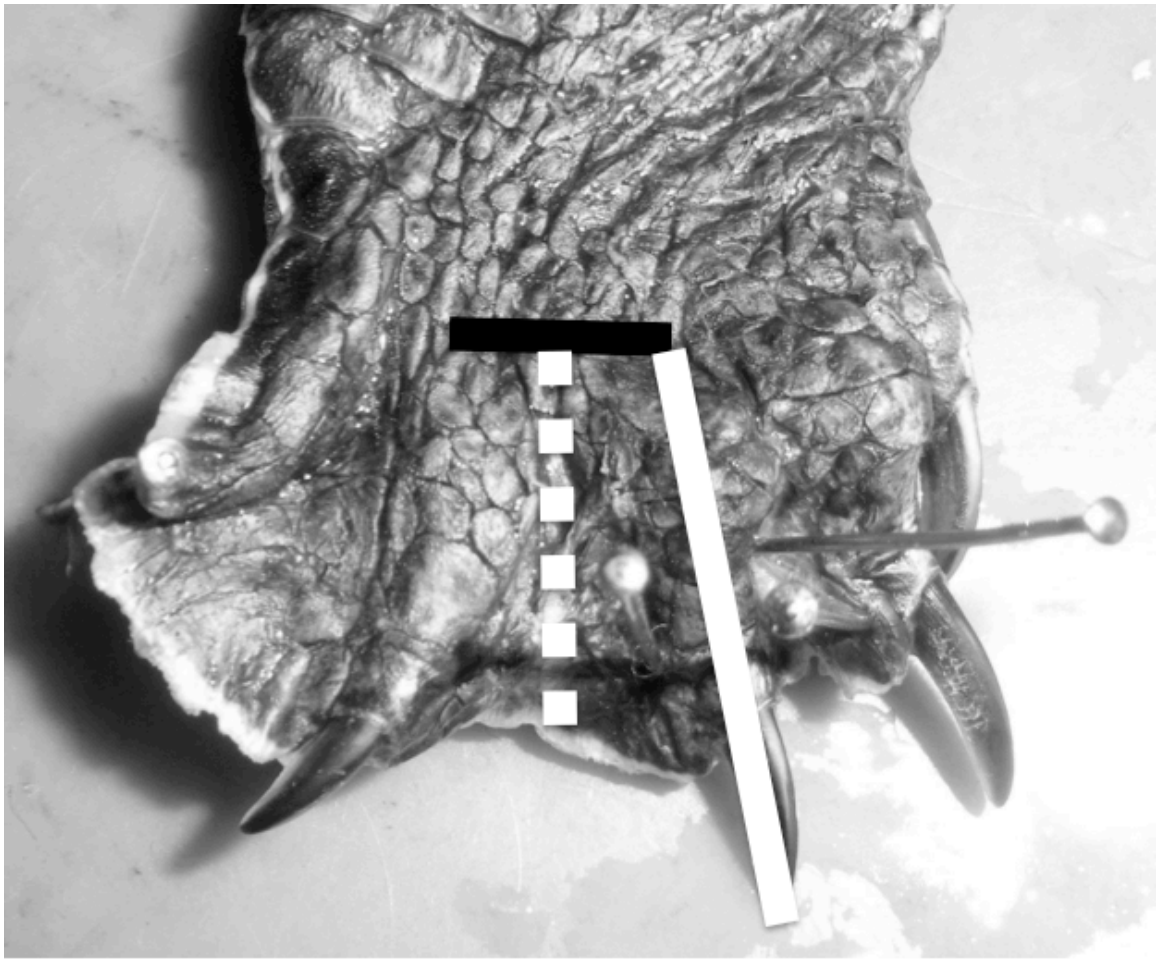

Fig. 2 – Pes measurements, illustrated on a foot of *Trachemys scripta elegans*. The black line represents the metatarsophalangeal joint. The white solid line represents the full digit length. The dashed white line represents the webbing length.

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The presence or absence of integumental structures such as tubercles and barbels was recorded as a binary variable (present/absent) on wet specimens. Tubercles are small protuberances that can show up anywhere on the body, while barbels develop below the mandible and on the ventral side of the neck.

Data Analysis

The distinctiveness of bottom-walking turtles, relative to aquatic swimmers or terrestrial walkers, was assessed by phylogenetic ANOVA. Phylogenetic ANOVA extracts F-statistics and other variables in the same manner as a conventional ANOVA, but significance is assessed by simulating data on a phylogeny. Phylogenetic ANOVA was conducted using the function in the "phytools" package of the statistical software R (R Core Team, 2013). Evolutionary simulations for the phylogenetic ANOVA were run 1000 times. After analysis, *P*-values were adjusted using the post-hoc test developed by Sture Holm (Holm, 1979). Three sets of tests were run on each variable - one separating out swimmers, bottom-walkers, and terrestrial taxa, one separating turtles based on habitat (water or land), and one separating turtles based on locomotor mode (walk or swim). The purpose of these comparisons was to dissect the differences between influences from ecology and function.

The 3-dimensional landmark coordinates used to assess turtle shell shape were subjected to a principal components analysis, and all significant PCs were used as input for a series of phylogenetic ANOVAs. Tail length was regressed against carapace length, and residuals were used as input for phylogenetic ANOVA.

Similarly, residuals were collected from digit length regressed against carapace length and webbing length regressed against digit length, and analyses were conducted on those residuals. The data for integumental structures was qualitatively recorded, then converted into binary categories (presence of integumental structures=1, no presence=0) and used as input in a phylogenetic ANOVA.

Results

Morphology

The shape PCA produced 10 significant PC axes (Fig. 3). Phylogenetic ANOVA on PC1 indicated differences between terrestrial taxa and all other locomotor styles ($F=77.0546$, $p<0.05$; Table I). This PC summarizes 62.9% of the variation within the shell morphology dataset. No significant differences were found on subsequent PCs. Terrestrial taxa tended to have shells that were taller dorsoventrally and shorter anterior to posterior than aquatic groups. Terrestrial taxa also had narrower plastra and aquatic species have shorter bridges (Fig. 3).

Table 1 – Results of post-hoc tests for differences between groups, conducted on PC1 for shell shape, following phylogenetic ANOVA.

T-statistic/ *P*-value	Aquatic	Bottom-walker	Marine	Terrestrial
Aquatic	X	-	-	-
Bottom-walker	-4.52/0.555	X	-	-
Marine	-3.26/0.555	-1.68/0.555	X	-
Terrestrial	11.66/0.025	13.66/0.006	6.80/0.028	X

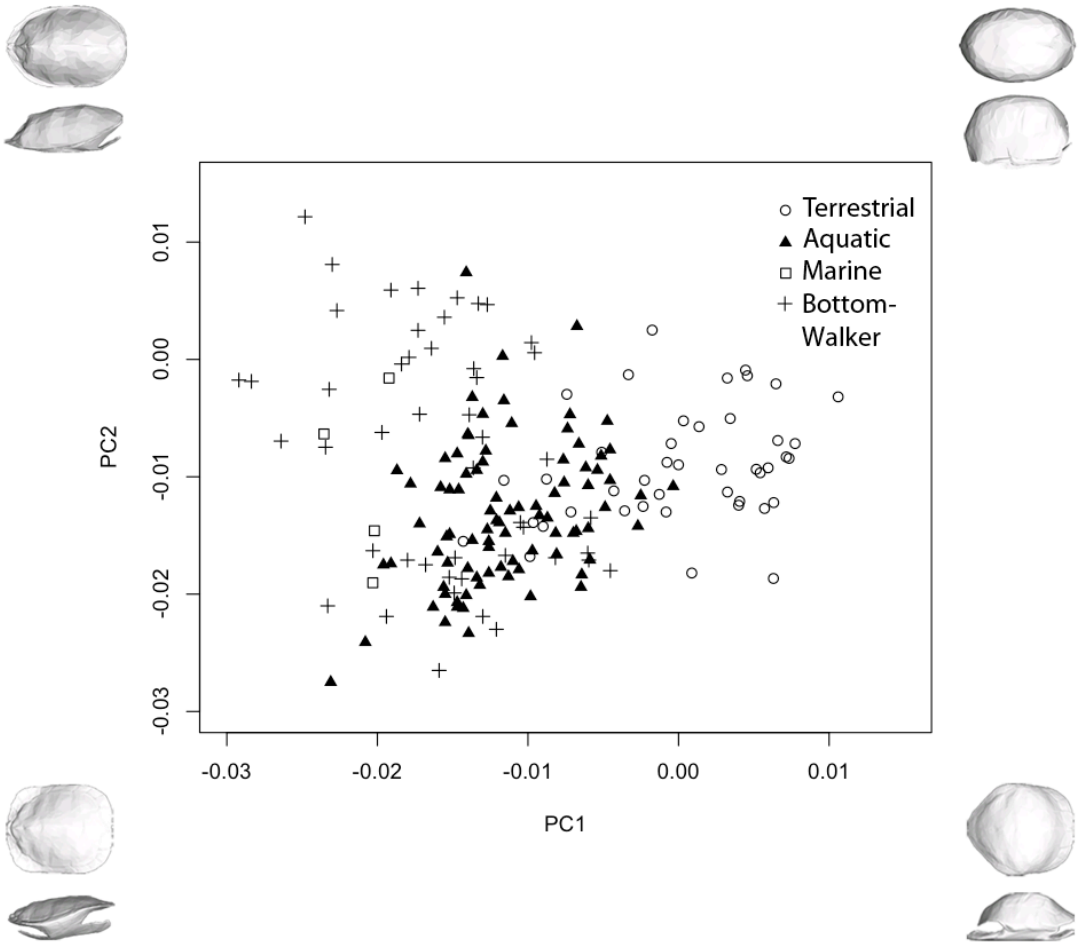

Fig. 3 - Morphospace plot of average species PC1 and PC2 values.

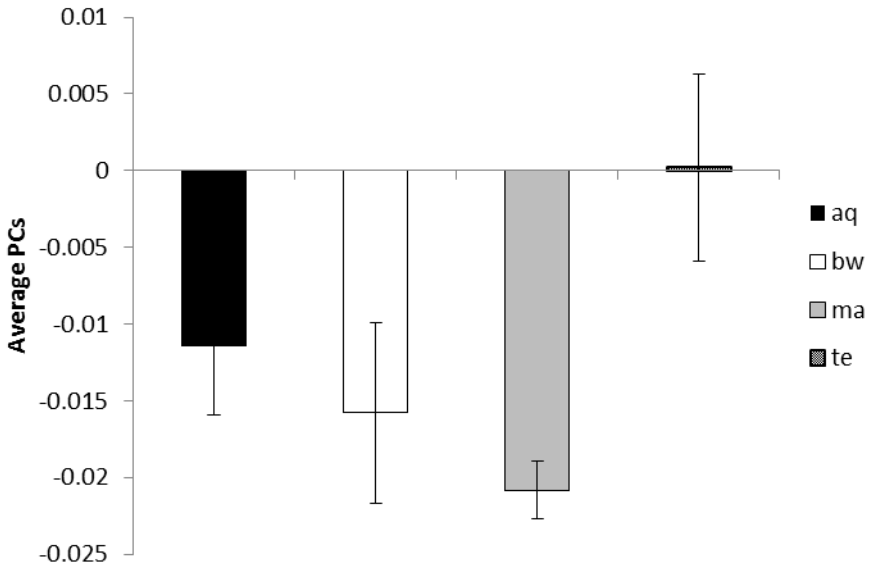

Fig. 4 – Average PC1 scores across standard groups.

Tail length

Phylogenetic ANOVA with standard ecological grouping indicated no significant differences among groups (F: 9.331002, p=0.299; Table 2). Locomotor mode and habitat grouping similarly yielded insignificant results.

Table 2 – Results of post-hoc tests for differences between groups, conducted on tail length residuals, following phylogenetic ANOVA

T-statistic/ *P*-value	Aquatic	Bottom-walker	Marine	Terrestrial
Aquatic	X	-	-	-
Bottom-walker	3.31/1.000	X	-	-
Marine	-0.93/1.000	-2.41/1.000	X	-
Terrestrial	-2.20/1.000	-5.10/0.858	-0.12/1.000	X

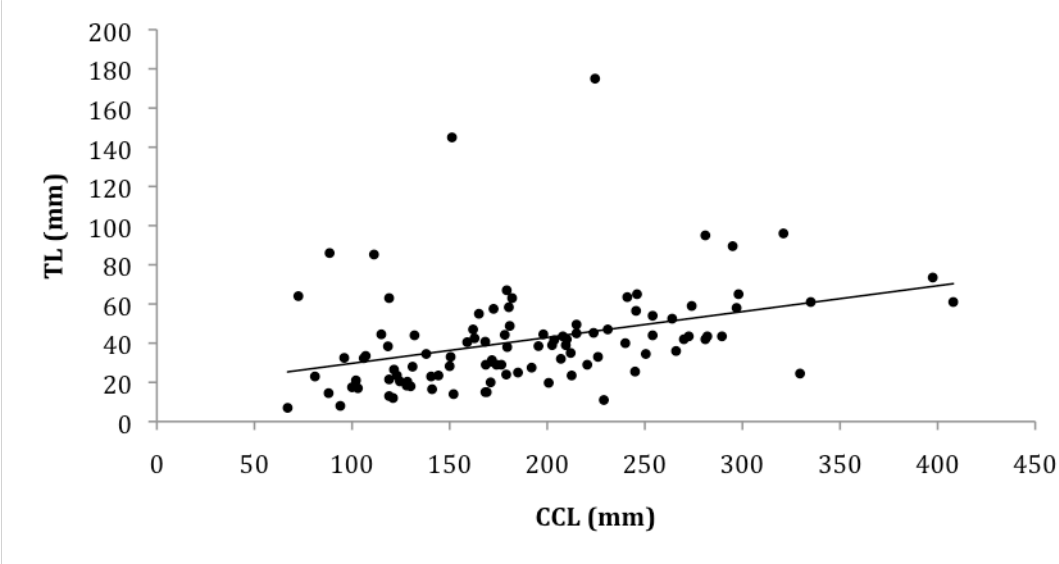

Fig. 5 – Scatterplot of tail length (TL) versus curved carapace length (CCL) with linear trendline.

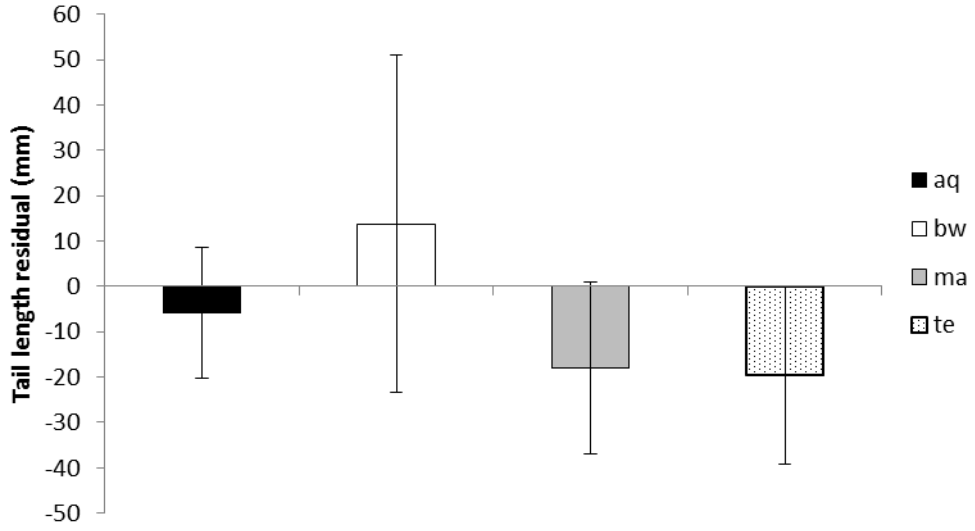

Fig. 6 – Average TL/CCL residual values across standard groups.

Digit Length

Phylogenetic ANOVA with standard ecological grouping yielded significant differences among groups (F: 28.88307, p=0.006; Table 3). Terrestrial turtles had significantly shorter digits than the aquatic species. Marine turtles were exempt from this test due to highly derived limb morphology and lack of superficially discernable metatarsophalangeal joints.

Table 3 – Results of post-hoc tests for differences between groups, conducted on digit length residuals, following phylogenetic ANOVA

T-statistic/ *P*-value	Aquatic	Bottom-walker	Terrestrial
Aquatic	X	-	-
Bottom-walker	1.10/0.610	X	-
Terrestrial	-6.25/0.018	-7.17/0.018	X

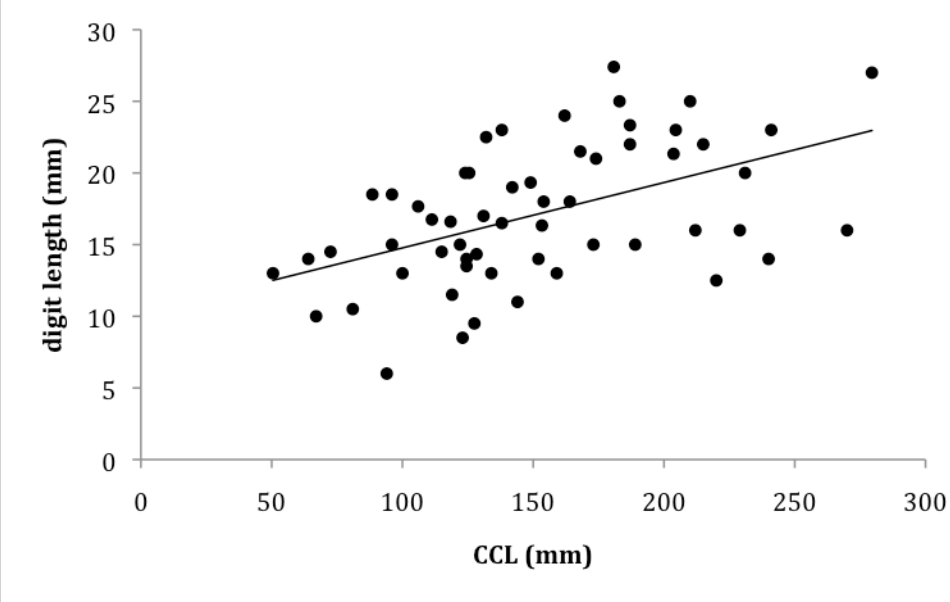

Fig. 7 – Scatterplot of digit length versus CCL with linear trendline.

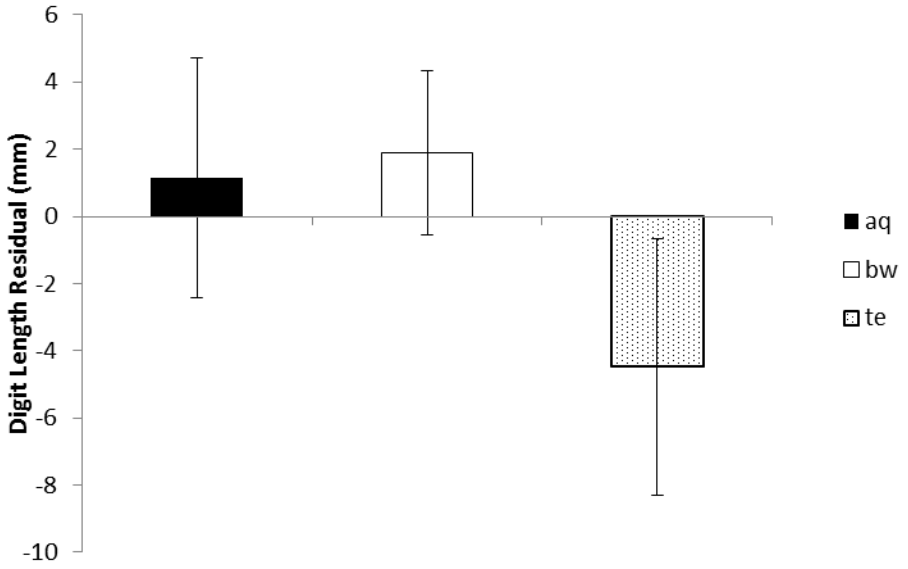

Fig. 8 – Average digit length/CCL residual values across standard groups.

Additional tests for habitat yielded significant differences between land-dwelling and water-dwelling species. (F = 56.32901, p=0.004). The additional ANOVA with locomotor mode as grouping did not show significant differences between walking species and swimming species. (p>0.05)

Digit Webbing Length

Phylogenetic ANOVA with standard ecological grouping yielded no significant results (F=0.701474, p=0.858; Table 4).

Table 4 – Results of post-hoc tests for differences between groups, conducted on webbing length residuals, following phylogenetic ANOVA

T-statistic/ *P*-value	Aquatic	Bottom-walker	Terrestrial
Aquatic	X	-	-
Bottom-walker	-0.41/1.000	X	-
Terrestrial	-1.18/1.000	-0.80/1.000	X

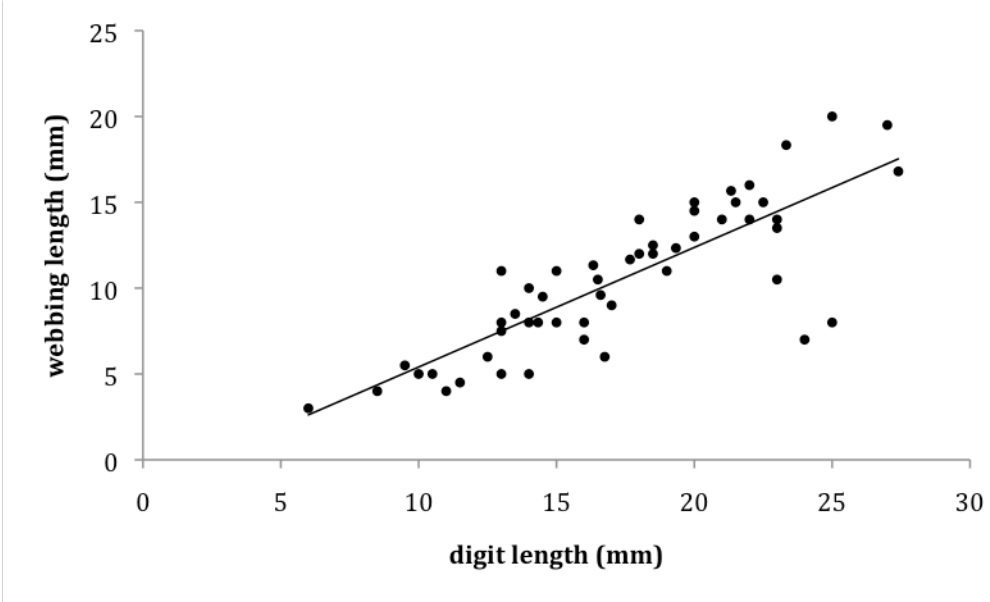

Fig. 9 – webbing length/digit length scatterplot with regression.

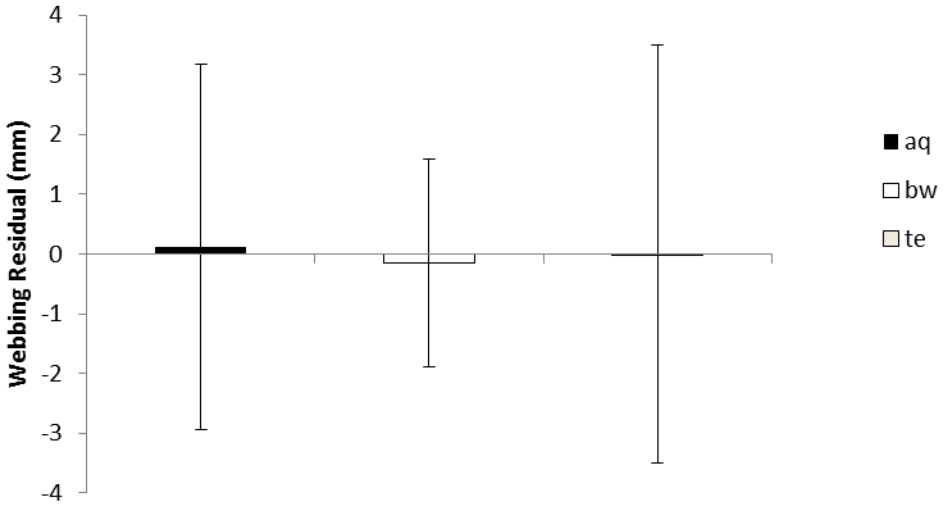

Fig. 10 – Average webbing length/digit length residual values across standard groups.

The additional tests with locomotor mode and habitat did not show any significant differences. (p>0.05)

Integument

Phylogenetic MANOVA with standard ecological grouping yielded significant results (F=20.43418, p=0.022; Table 5); Bottom-walkers were significantly different from terrestrial turtles.

Table 5 – Results of post-hoc tests for differences between groups, conducted on integumental rating, following phylogenetic ANOVA

T-statistic/ *P*-value	Aquatic	Bottom-walker	Terrestrial
Aquatic	X	-	-
Bottom-walker	3.12/0.208	X	-
Terrestrial	-3.59/0.208	-6.39/0.045	X

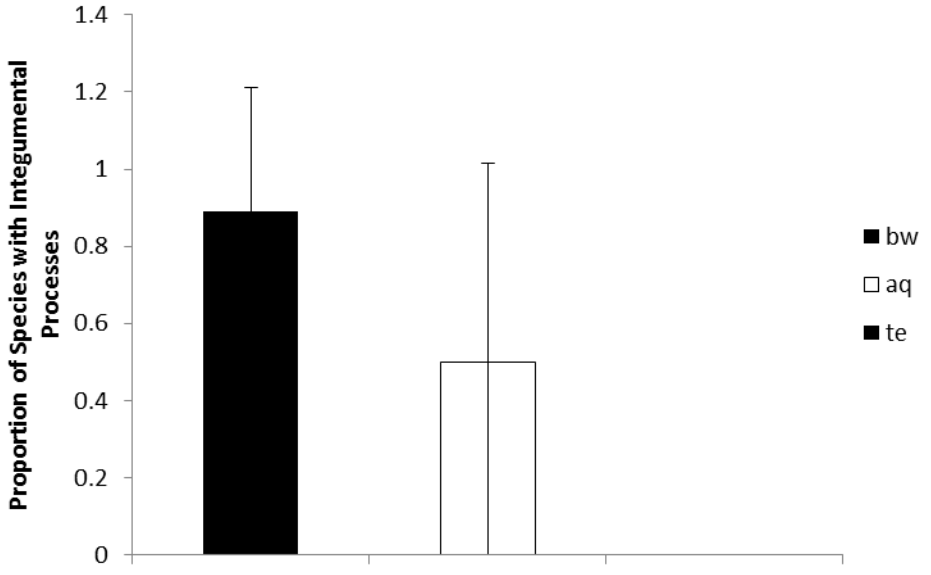

Fig. 11 – Proportion of species with integumental processes.

The additional grouping of habitat also yields significance (F=26.13636, T=5.11, p=0.033). The additional grouping of locomotor mode did not yield significance (F=0.04805014, p=0.907).

Discussion

Bottom-walkers were not significantly different from any other group in terms of shell morphology. Terrestrial turtles differed significantly from all other groups. Hence, bottom-walking turtles are neither distinct from other ecological or function categories of turtles, nor are they more similar to terrestrial taxa, as predicted.

Analyses on tail length did not indicate any significant differences between groups. This means that bottom-walkers did not have significantly longer (or shorter) tails than any other group. Between all groups, average relative tail length was surprisingly consistent.

Terrestrial turtles proved again to be significantly different from all other groups in terms of digit length. Terrestrial turtles had shorter pes digits than any other group. Bottom-walkers were not shown to be significantly different from any other group, and thus bottom-walker digit length was not significantly different than that of other aquatic species. The hypothesis was that a decreased need for swimming in bottom-walkers would in turn allow for less “paddle”-like pes, and thus the digits would be shorter. It appears that aquatic environments remain as a strong selective pressure insofar that of the bottom-walkers still facilitate drag-

based pes propulsion. It should be noted that some species, such as snapping turtles, which have been reported to never swim (Willey and Blob, 2004), have been observed swimming in captivity (C. Stayton, *pers. comm.*) – perhaps swimming is not as uncommon in bottom-walkers as is currently understood. The test conducted grouping by habitat similarly showed terrestrial turtles to be significantly different in terms of digit length than the aquatic species. The webbing analyses did not indicate any significant differences between groups, surprisingly, meaning that all groups had consistent relative webbing length.

Integumental analyses showed that bottom-walkers were different from terrestrial turtles in terms of the presence of integumental processes. Tubercles and barbels were most common on bottom-walkers, although many specimens also had keratinized ridges upon their antebrachium, possibly to aid in digging in soft mud or bottoms of waterways. Members of Kinosternidae and Chelydridae had the most intricate patterns of bumps and tubercles across the entire body. However, the chelid *Chelus fimbriatus*, the mata mata turtle, is perhaps the most outstanding individual, its head and body covered with fringed crests of integument. Many bottom-walkers, even without the same degree of integumentary processes, still had presence of 1-3 barbels underneath their mandible. Similarly, some bottom-walkers did not have any tubercles or barbels, but had rough, corrugated skin over the majority of the body. In the phylogenetic ANOVAs, terrestrial turtles differed significantly from only bottom-walkers. However, neither bottom-walkers nor terrestrial turtles differed significantly from aquatic, swimming turtles. This suggests a gradient of selective pressures for integumental processes: bottom-

walkers with the greatest pressure and presence, terrestrial turtles with the least, and aquatic, swimming turtles in between. The test run again with habitat groups showed significant differences between water - and land - dwelling turtles. Here is the only case where bottom-walkers significantly differed from terrestrial species but aquatic species did not.

From a more functional point of view, integumental processes like tubercles and barbels are known to function as sensory structures, and they are also used in crypsis. Bottom-walkers appear to not swim as much as other aquatic species, so the selective pressure to improve hydrodynamicity is reduced. Other aquatic species may have integumental processes, but these are reduced due to the conflicting pressure of hydrodynamicity. Within the additional test of habitat, water-dwelling turtles were found to be significantly different from land-dwelling turtles, meaning water-dwelling turtles had more integumental processes than terrestrial turtles. If these integumental structures have chemosensory function, they would only be effective in water. If these structures have tactile-sensory function, they could benefit terrestrial turtles as well. Terrestrial turtles had no structures, possibly due to highly-keratinized skin that prevents dessication. This skin type would hinder the growth of sensitive integumental structures.

Overall, I did not find strong support for any hypotheses. Bottom-walker shells were not found to be significantly different than any other group aside from terrestrial turtles. This corroborates the findings of Claude (2003), further showing that aquatic and terrestrial turtle shells differ in morphology, but fails to show any additional differences within aquatic species. No groups were found to have tails to

be significantly longer than any other group. This hypothesis was based on anecdotal observations of particular groups that are known to bottom walk (e.g., Chelydridae, Platysternidae, and Chelidae). Despite the specimens of these particular groups actually having relatively long tails, it appears that they are not representative of bottom-walkers overall.

Terrestrial turtles have been shown to have relatively stronger, if less streamlined, shells than those of aquatic turtles (Stayton, 2011). Our results suggest that bottom-walking turtles will be similarly less strong but more streamlined. However, many-to-one mapping of form onto function means that even small differences in shell shape can lead to large differences in function – future work could investigate bottom-walker shell mechanics. However, considering that the aquatic and bottom-walker shells did not differ in shape, it is unlikely that they differ in mechanics.

Overall, ecological habitat has a stronger influence on morphology than locomotor mode, with regards to bottom-walking turtles. Bottom-walkers, despite adopting a different mode of locomotion than other aquatic turtles, still apparently experience similar selective pressures from inhabiting in an aquatic environment. Results from the shell morphology analysis further confirm the differences between aquatic and terrestrial turtle shells. This implies that bottom-walkers, although subset of aquatic turtles on the basis of locomotor mode, are not morphologically different enough to be considered a separate group. Morphologically, bottom-walkers group with swimming aquatic turtles. Perhaps bottom-walking represents a novel locomotor mode that has yet to evolve to be distinctive from ancestral an

ancestral swimming mode. However, many lineages of bottom-walkers, such as Chelydridae and Kinosternids, are some of the oldest families of turtles (Ericson, 1973; Gaffney, 1975). Alternatively, speed and efficient movement may not be as much of an issue for these turtles as was initially thought. It appears that bottom-walkers are vastly more strongly affected by ecology. When considering the integumental tests, generalization of turtles into habitat groups such as aquatic and terrestrial seems inappropriate. In this regard, a spectrum seems more appropriate. Further investigation using different habitat groups or with a particular family is highly encouraged.

This study demonstrates that ecology has more of an effect than function does on turtle morphology. Bottom-walking gait kinematics may be different from terrestrial gait kinematics. Aquatic turtle bodies are approximately neutral density with water, therefore bottom-walking turtles may implement a mode more similar to punting, a mode of seafloor locomotion used by crabs and rays (Koester and Spirito, 2003; Martinez et al., 1998). Because of this, we should be wary of deciding which selective pressures are important, just based on *common* locomotor modes. Less-used locomotor modes may contribute more to morphology than previously thought; bottom-walkers may not be seen swimming much of the time, but the few instances in which that mode is necessitated places pressure to maintain shell morphology comparable to that of aquatic turtles. In this case, ecology has such a greater influence, it can practically be considered as a proxy for selective pressures. This basic trend could be applied to other animals that inhabit the same environments to help attribute morphology to similar selective pressures.

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